

REVISION OF *ANCYLOCERAS BIPUNCTATUM* SCHLÜTER, 1872
(CEPHALOPODA, AMMONOIDEA) AND DISCUSSION OF THE
VALIDITY, PHYLOGENY AND LIMITS OF THE GENUS
NEANCYLOCERAS SPATH, 1926

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(With 10 figures)

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ABSTRACT

The syntypes and topotype material of *Ancyloceras bipunctatum* Schlüter, 1872, the type species of the genus *Neancyloceras* Spath, 1926, are described and illustrated photographically. Schlüter's figures are misleading, being partially based on idealized reconstructions. Even if the effects of post-depositional deformation are taken into consideration, it appears that coiling in *Ancyloceras bipunctatum* as here interpreted may vary from open ancyloceratid to aspinocera-tid or crioceratid. *Neancyloceras* does not merit separation from *Exiteloceras* Hyatt, 1894, nor do *Axonoceras* Stephenson, 1941, or *Exicrioceras* Anderson, 1958. Affinities of *Exiteloceras* with *Neocrioceras* Spath, 1921, and *Pseudoxybeloceras* Wright & Matsumoto, 1954, are discussed and a possible common origin in the Turonian is postulated. Species previously referred to *Neancyloceras* are reviewed.

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INTRODUCTION

Two or, possibly, all three of Schlüter's figured syntypes of *Ancyloceras bipunctatum* (Schlüter 1872: 98, pl. 29 (figs 1-3)) (Fig. 1 (1-3 herein)) as well as a number of other possible syntypes and topotype material were located in the collections of the Geologisch-Paläontologisches Institut und Museum der Georg-August Universität, Göttingen. Examination of Schlüter's original and topotype material allows better definition of the species and discussion of the validity, origin, phylogeny, and limits of the genus *Neancyloceras* Spath, 1926, of which it is the type species.

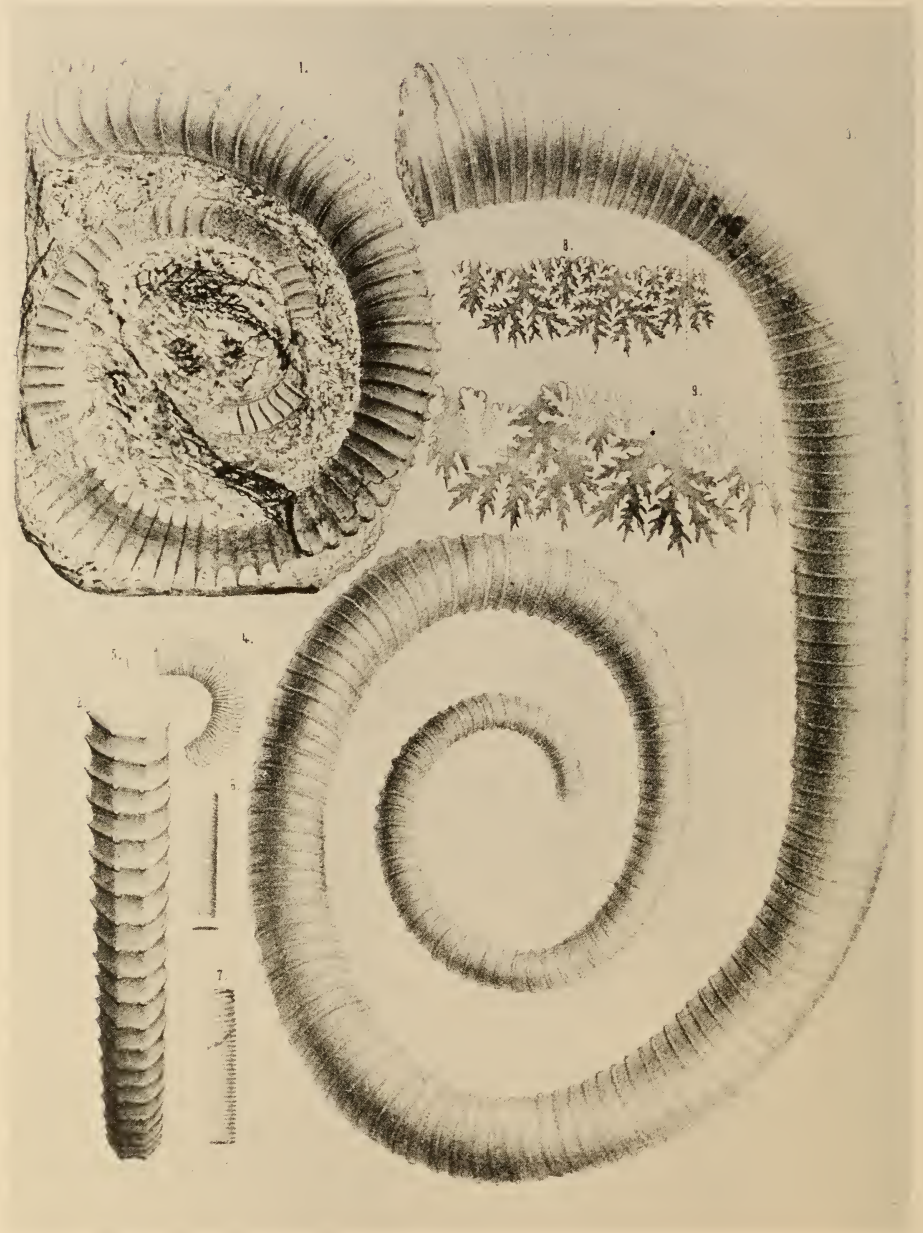


Fig. 1. Copy of Schlüter's (1872) original plate 29. $\times 0,67$.

SYSTEMATIC DESCRIPTION

Ancyloceras bipunctatum Schlüter, 1872

Figs 1 (1-3), 2-8 A-E, 9

- Ancyloceras bipunctatum* Schlüter, 1872: 98, pl. 29 (figs 1-3) (erroneously spelt *bipunctum* in explanation to plate figures).
- Ancyloceras bipunctatum* Schlüter: Wegner, 1905: 210. Nalivaiko, 1936: 35, pl. 16 (fig. 39).
Michailov, 1951: 88, pl. 16 (figs 66-71). Pasternak, 1954: 157, text-fig. p. 158.
- Neancyloceras bipunctatum* (Schlüter): Naidin, 1959: 182, pl. 3 (fig. 6). Hancock, 1961: 30.
Giers, 1964: 283. Blank *et al.* 1974: 169.

Type

The lectotype, herein designated, is the specimen figured by Schlüter (1872, pl. 29 (fig. 1)) from the Campanian of Ahlten, near Hanover, West Germany, housed in the collections of the Geologisch-Paläontologisches Institut und Museum der Georg-August Universität, Göttingen, GPIG Orig. 65-10.

Material

The paralectotype figured by Schlüter (1872, pl. 29 (fig. 3)) (catalogue number GPIG Orig. pending), a specimen tentatively identifiable with the third figured specimen in Schlüter (1872, pl. 29 (fig. 2)) (GPIG Orig. 65-11), and forty-six other specimens, all from the same locality and in the same collections, were available for study. Schlüter's descriptions were based on five specimens in the collections at Göttingen, and on a sketch of one of the specimens in the collection of Mr Witte of Hanover. The latter collection was subsequently presented to the above-mentioned Institute in Göttingen (see Schlüter 1876: 181 footnote) and incorporated in their collections. Apart from the lectotype and paralectotype(s), it is impossible to determine from the labelling which specimens were Schlüter's original syntypes, and which belonged to the Witte collection.

*Descriptions**Lectotype GPIG Orig. 65-10 (Fig. 2A)*

Schlüter's illustration of the lectotype is reversed and much restored. Only half of the outer whorl and less than a quarter of the inner whorls are actually preserved as internal moulds. The rest of the specimen is indicated only by brown (?limonitic) stained impressions. The double row of ventral tubercles in the actual specimen is by no means as pronounced as in the lithograph, nor are both rows as clearly exposed as the figures suggest. The strongly flared ribbing (as indicated on the lower half of Schlüter's figure) is also idealized. The last part of the whorl seems to detach itself from the open spiral. The last septum is in the last half of this whorl.

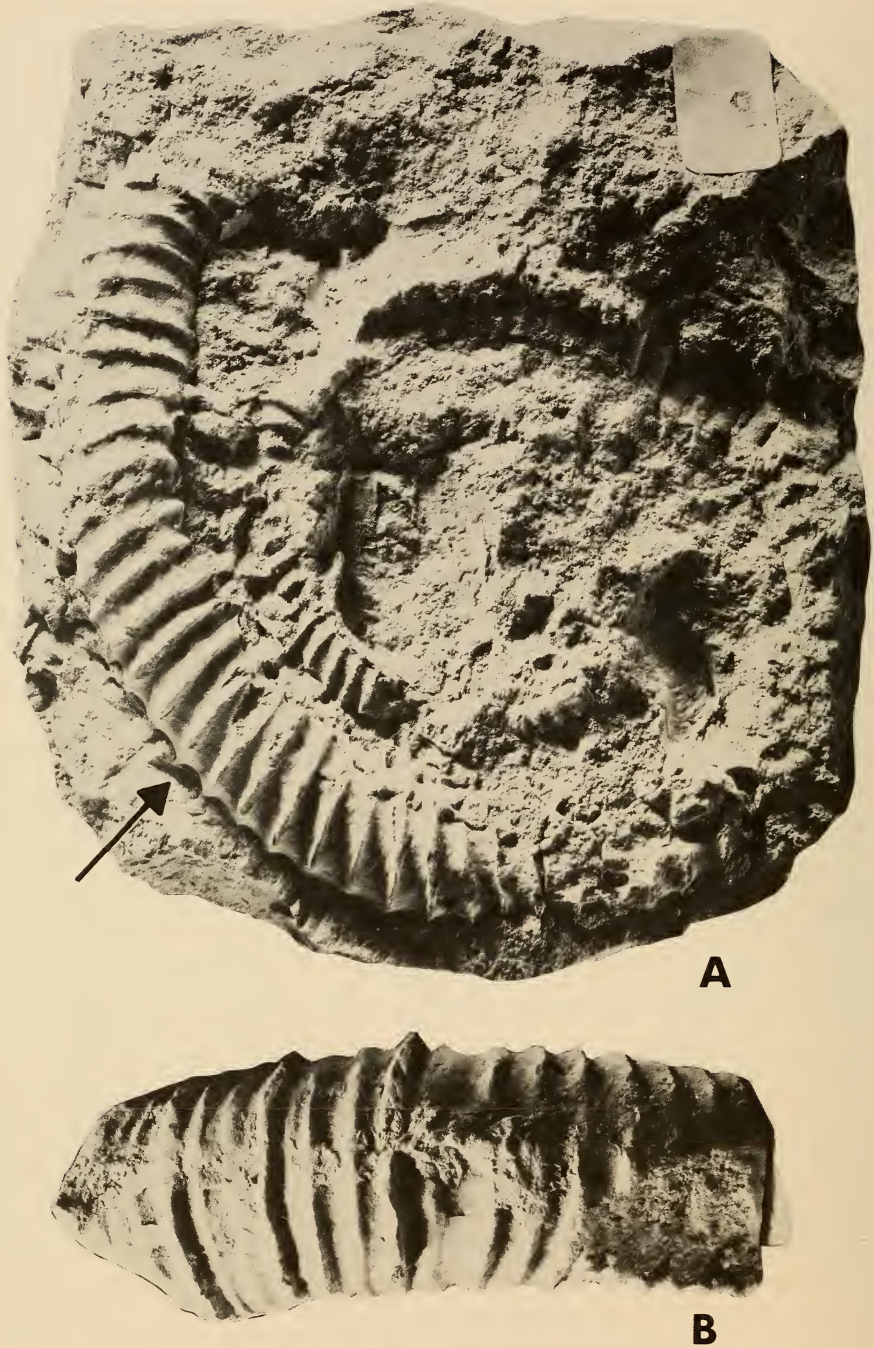


Fig. 2. *Exiteloceras bipunctatum* (Schlüter, 1872).

- A. The lectotype, figured in reverse by Schlüter (1872, pl. 29 (fig. 1)) GPIG Orig. 65-10.
 B. A large, slightly curved body chamber fragment with differentiated ribbing. GPIG-8.
 Both specimens from the Upper Campanian of Ahlten, West Germany. $\times 1$.

Paralectotype GPIG Orig. pending (Figs 3, 4A)

According to Schlüter (1872, pl. 29 (fig. 3)) the figure of the paralectotype was based on a sketch of a complete specimen in the possession of Mr Witte of Hannover. Part of the shaft and open hook in the figure can be identified with a crushed specimen (GPIG Orig. pending). The loosely coiled inner whorls of the sketch on which the lithograph was based are very similar to those of GPIG-2 (Fig. 5A), but this specimen does not belong to the same individual as GPIG Orig. pending, nor do any of the other available specimens. It must be assumed either that the initial inner whorls of paralectotype GPIG Orig. pending are lost, or that Witte's sketch from which Schlüter's lithograph was constructed was, in fact, a synthetograph based on GPIG Orig. pending and GPIG-2 or another specimen similar to it such as GPIG-3 (Fig. 6). Whatever the case may be, Schlüter's illustration of the shaft and hook is misleading. Ribbing is not uniform throughout as the illustration suggests, but stronger ribs separated by a variable number of normal ribs are present. These major ribs are bituberculate, like the normal ribs. At the adapical end of the shaft the major ribs are separated by about eight normal ribs, but towards the hook the major ribs become more prominent, their tuberculation less distinct, and intermediaries decrease to as little as two. Traces of the last septa are visible near the lower end of the straight shaft.

?Paralectotype GPIG Orig. 65-11

A slightly crushed specimen, GPIG Orig. 65-11 (Fig. 5B-D) is of the same size as the third specimen figured by Schlüter (1872 pl. 29 (fig. 2)), but due to lack of documentation the author is unable to confirm whether or not this is indeed the figured specimen in its unrestored form. None of the available specimens shows the perfect bilateral symmetry as seen in Schlüter's figures, suggesting that asymmetrical whorl section and ornament were the norm rather than the exception, as will be discussed further.

Topotype material

Two specimens, GPIG-2 (Fig. 5A) and GPIG-3 (Fig. 6) show the early, irregular crioceratitid coiling as seen in the lectotype. GPIG-3 is the most complete and has a somewhat irregular mode of coiling. Three-quarters of the outer whorl is occupied by body chamber. The last part of the body chamber appears to uncoil slightly and then recoil again. Only the last rib is thickened. GPIG-2 (Fig. 5A) has a virtually circular inner whorl as found in the lectotype, but a body chamber that uncoils and then recoils similar to that of GPIG-3. Here only the last half whorl is body chamber, and thickened ribs do not occur.

All the specimens are deformed to some extent; however, it does appear that the whorl section and ornament are asymmetrical in the majority, with tuberculation displaced towards one side. This suggests that the inner phragmone whorls were coiled in a low, perhaps irregular or elliptical helix rather than in one plane. At the smallest whorl diameter preserved (6 mm), the



Fig. 3. *Exiteloceras bipunctatum* (Schlüter, 1872).
The paralectotype, GPIG Orig. pending upon which
Schlüter's (1872, pl. 29 (fig. 3)) reconstruction was partially
and incorrectly based. From the Upper Campanian of
Ahlden, West Germany. $\times 0,77$.

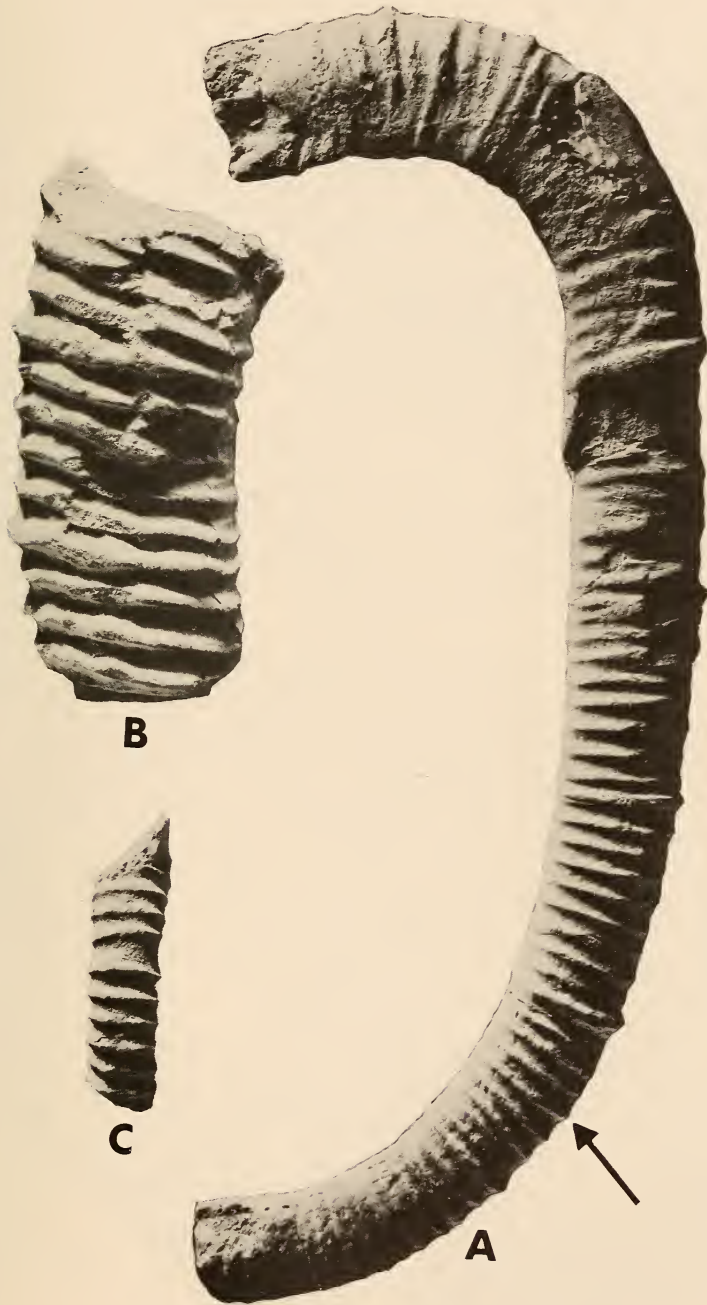


Fig. 4. *Exiteloceras bipunctatum* (Schlüter, 1872).

A. The paralectotype, GPIG Orig. pending upon which Schlüter's (1872, pl. 29 (fig. 3)) reconstruction was partially and incorrectly based. B. Topotype specimen GPIG-5; a straight body chamber fragment. C. Topotype specimen GPIG-12 showing shallow, wide constriction.

All specimens from the Upper Campanian of Ahlten, West Germany. A $\times 0,77$; B-C $\times 1$.



Fig. 5. *Extieloceras bipunctatum* (Schlüter, 1872).
 A. Topotype specimen GPIG-2. Arrow points to last visible septum. B-D. Possible paralectotype GPIG Orig. 65-11 (see Schlüter 1872, pl. 29 (fig. 2)).
 Both specimens from the Upper Campanian of Ahlten, West Germany. $\times 1$.



Fig. 6. *Exiteloceras bipunctatum* (Schlüter, 1872). Topotype specimen GPIG-3. Arrow points to last visible septum. From Ahlten, West Germany. $\times 1$.

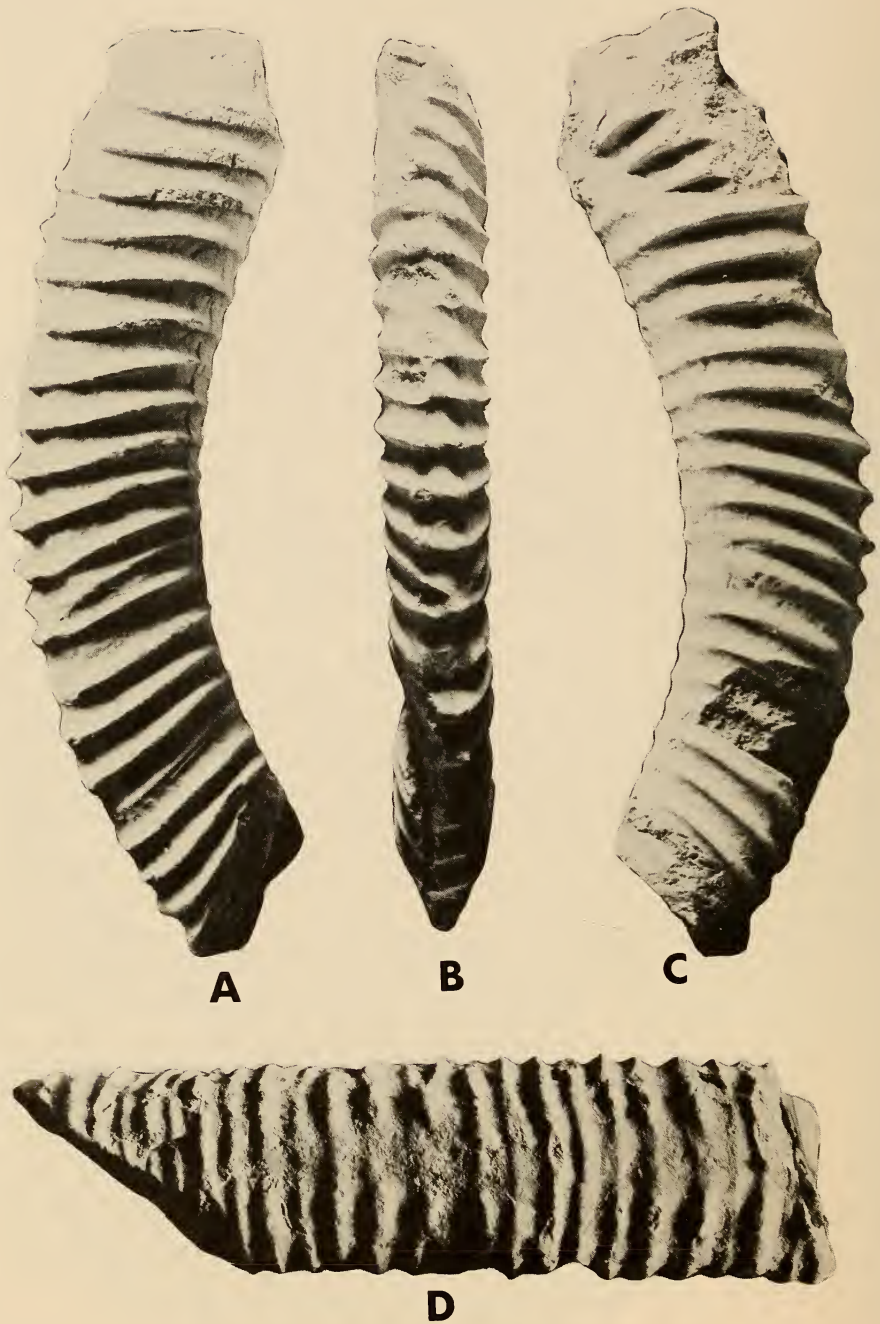


Fig. 7. *Exiteloceras bipunctatum* (Schlüter, 1872).
A-C. Topotype specimen GPIG-9. D. Straight body chamber fragment GPIG-10.
Both specimens from the Upper Campanian of Ahlten, West Germany. $\times 1$.

whorls are still coiled, and do not show straight or otherwise aberrant early coiling. GPIG-16 (Fig. 8D-E) shows labeceratid coiling but this is probably due to post-mortem deformation.

On the phragmocone, rib density is generally between four and five per maximum whorl diameter, but may be as high as eight. Some specimens, e.g. GPIG-12 (Fig. 4C) and GPIG-13 (Fig. 9B), show slight irregularities in ribbing which may be interpreted as shallow constrictions. The sharp-crested, slightly rursiradiate, bituberculate and even ribbing is characteristic of the major part of the shell. Stronger ribs appear only on the last part of the phragmocone and on the body chamber in some specimens.

Straight and curved body chamber fragments can be identified. GPIG-5 (Fig. 4B), GPIG-10 (Fig. 7D), GPIG-11 (Fig. 9D), and GPIG-17 (Fig. 9A) are straight or slightly curved body chamber fragments identifiable with the open ancyloceratid paralectotype, GPIG pending (Figs 3, 4A). GPIG-11 (Fig. 9D) is of interest in not having major ribs. GPIG-8 (Fig. 2B) and GPIG-9 (Fig. 7A-C) are large, curved body chamber fragments; the former has distinct differentiated ribbing. GPIG-17 (Fig. 9A) is a body chamber fragment much larger than any of the other specimens.

Indistinct traces of trifid lobes are present on the lower ends of the paralectotype GPIG pending and GPIG-3.

DEFINITION OF THE SPECIES

As can be seen from the description of the original and topotype material, there is considerable variation in the coiling, ornament, and size of *Ancyloceras bipunctatum*. Even if the effects of the post-mortem deformation are taken into consideration, coiling of the body chamber ranges from distinctly open ancyloceratid to possibly aspinoceratid or crioceratid. Unmistakable ancyloceratid forms include the paralectotype GPIG pending (Figs 3, 4A), and parts of straight shafts such as GPIG-5 (Fig. 4B), GPIG-7 (Fig. 9C), GPIG-10 (Fig. 7D), and GPIG-11 (Fig. 9D). The last septum in the paralectotype GPIG pending is located in the lower end of the straight shaft. In the lectotype GPIG-Orig. 65-10 (Fig. 2A) half of the outer whorl is body chamber, whereas in GPIG-3 (Fig. 6) three-quarters of the outer whorl is body chamber. This, together with the presence of such large body chamber fragments as GPIG-8 (Fig. 2B) and GPIG-9 (Fig. 7A-C), suggests crioceratid or aspinoceratid coiling for some specimens rather than distinct open ancyloceratid coiling as suggested by Schlüter's reconstructed figure.

The relationship between these different modes of coiling is obscure. It is partially due to post-mortem deformation, but may also be a manifestation of dimorphism or, less probably, extreme intraspecific variation due to the fact that the material is from more than one stratigraphic horizon. Schlüter (1876: 248 and footnote) had already expressed doubts on whether or not the material from Ahlten all belonged to one zone.

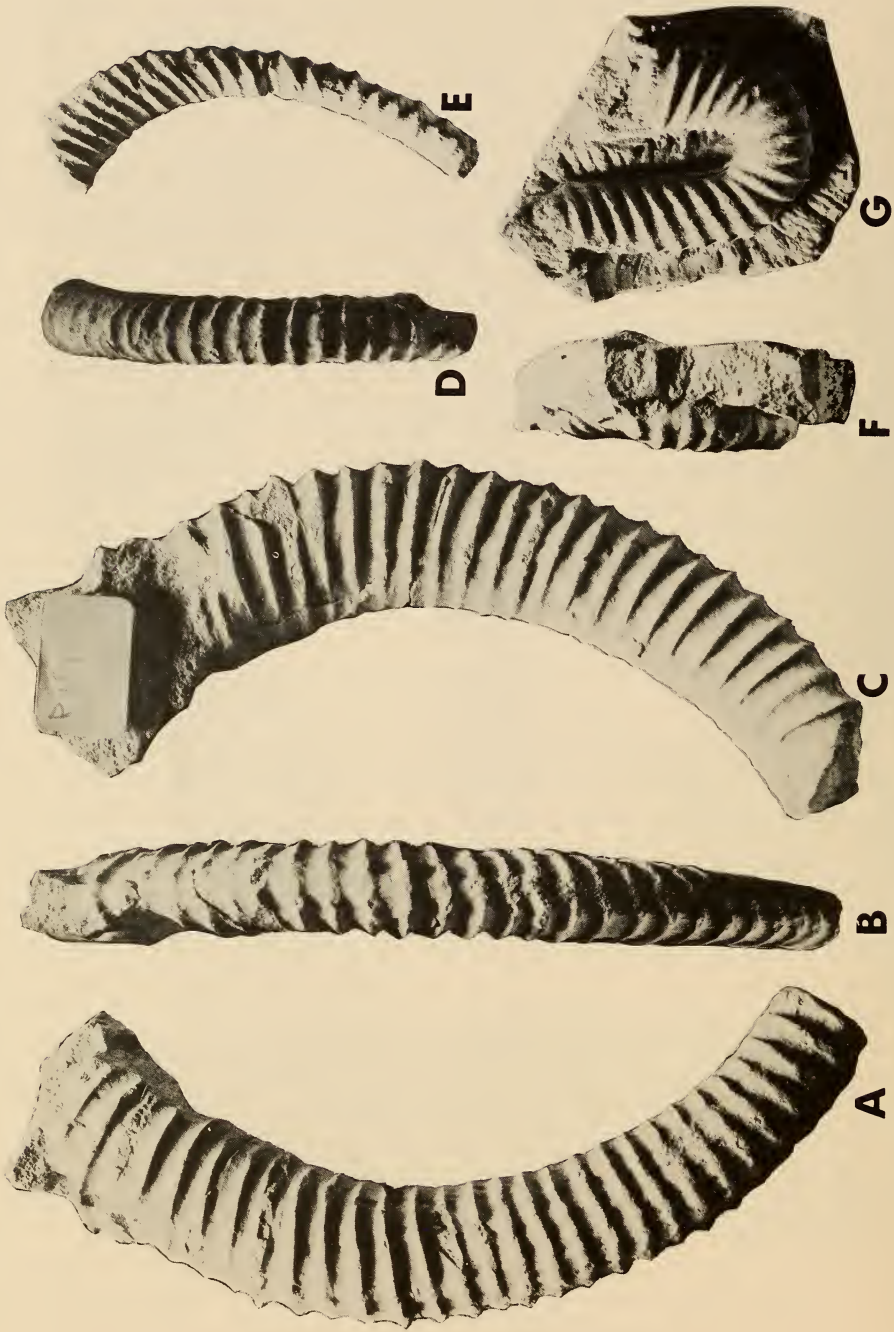


Fig. 8. A-C. *Exiteloceras bipunctatum* (Schlüter, 1872). Typical phragmocone fragment. GPIG-14. D-E. *Exiteloceras bipunctatum* (Schlüter, 1872). GPIG-16, specimen with labeceratid coiling due to deformation. F-G. *Pseudoxylloceras (Parasolenoceras) interruptus* (Schlüter, 1872). The holotype by monotypy GPIG Orig. 65-13. All specimens from the Upper Campanian of Ahlten, West Germany. $\times 1$.

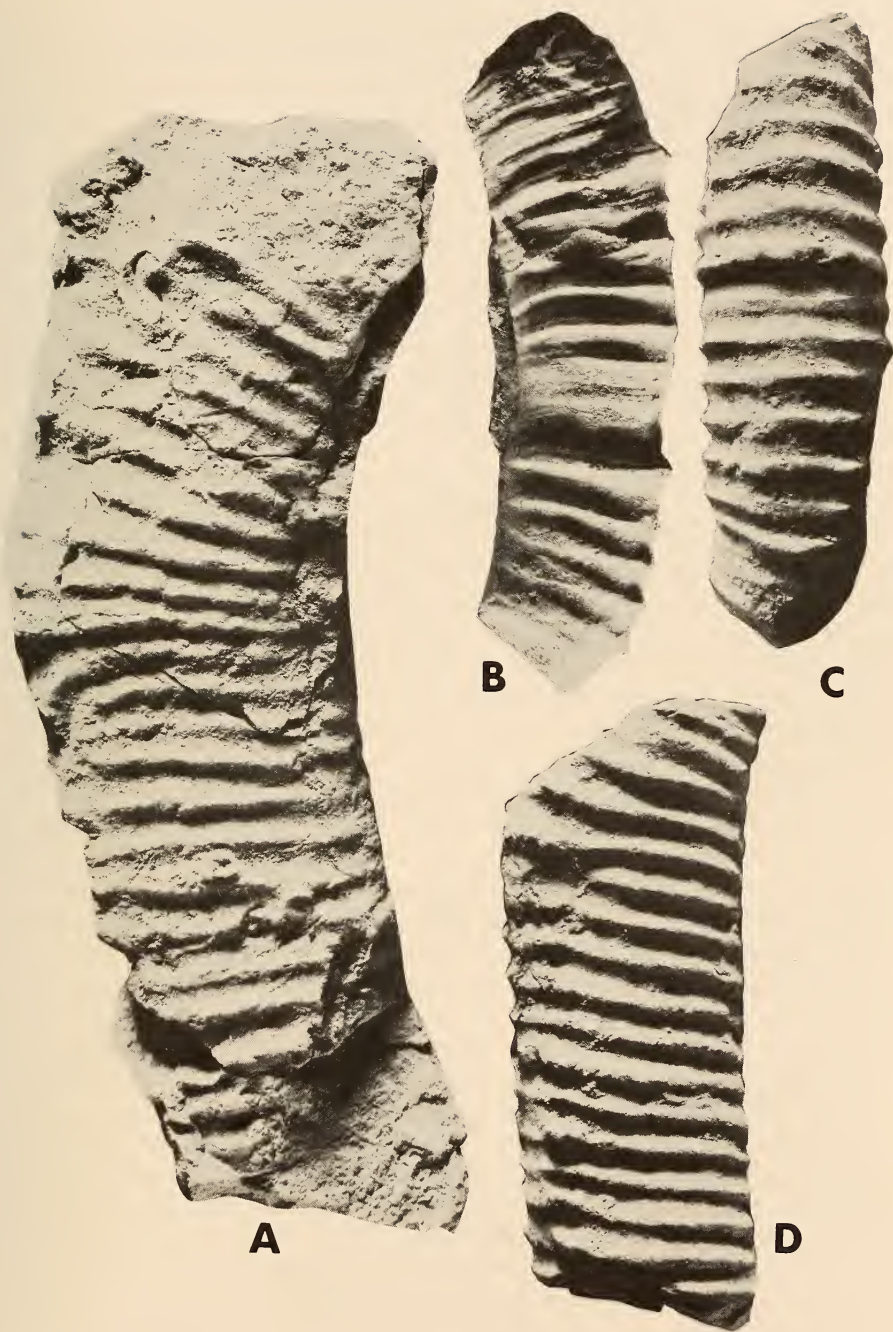


Fig. 9. *Exiteloceras bipunctatum* (Schlüter, 1872).

A. Gigantic body chamber fragment GPIG-17. B. Body chamber fragment with differentiated ribbing and shallow constriction. GPIG-13. C. Slightly curved body chamber fragment GPIG-7. D. Straight body chamber fragment GPIG-11.

All from the Upper Campanian of Ahlten, West Germany. $\times 1$.

On the basis of the material available, it is not possible to give a definitive answer to these questions, and all the specimens are included in the same species. Specimens figured by Michailov (1951: 88, pl. 16 (figs 66–71)) as *Ancyloceras bipunctatum* also suggest an open, crioceratitid or aspinoceratid mode of coiling in some specimens, although a straight fragment was also figured.

From the descriptions above, *Ancyloceras bipunctatum* may be defined as probably being dimorphic. The shell probably has an initial, loosely coiled, shallow helix with similar ribbing, and tubercles displaced slightly to one side. Wide, shallow constrictions may occur. This is followed in smaller specimens by an open, ancyloceratid shaft and hook, and in the larger specimens by irregular, crioceratitid or aspinoceratid coils. Major ribs occur variably on the last part of the phragmocone and on the body chamber.

GENERIC STATUS

Spath (1926: 80) erected the genus *Neancyloceras* merely by citing *Ancyloceras bipunctatum* Schlüter, 1872, as type species and added that 'this stock of the *mucronata* zone is obviously distinct from *Oxybeloceras* Hyatt, with which the writer (loc. cit. Zululand, 1921, p. 254) had formerly united it'. Later, Spath (1953: 16) added that '*Oxybeloceras* and *Neancyloceras* are distinguished by their regular and very sharp costation' and (Spath 1953: 17) '*Ancyloceras* (?) *pseudoarmatum* Schlüter . . . is probably a somewhat homoeomorphous development of *Neancyloceras*'.

Wright (1957: L227) interpreted *Neancyloceras* as differing 'from open-whorled species of *Glyptoxoceras* in less regular coiling and bituberculate periphery'. Comparisons with *Glyptoxoceras* as suggested by Wright are superficial, as no true glyptoxoceratid is bituberculate, and coiling is by no means as regular as is claimed. Comparisons with *Neoglyptoxoceras* Collignon can be ignored on the same grounds.

Interpreted in terms of the type species as here defined, *Neancyloceras* bears closer affinity to the Upper Cretaceous genera *Exiteloceras* Hyatt, 1894, *Axonoceras* Stephenson, 1941, and *Exicrioceras* Anderson, 1958. Differences between these taxa are slight and it is doubtful if they even merit generic separation. All generally have simple bituberculate ribbing.

Axonoceras Stephenson, 1941, (type species *Axonoceras multicostratum* Stephenson, 1941) is best known from Texas (Stephenson 1941), ?California (Anderson 1958), Angola (Haas 1943), and Madagascar (Collignon 1971). All specimens are small—less than 50 mm in diameter. *Axonoceras* is identified mainly by the irregular coiling of the inner whorls, that is, uncoiling and recoiling, resulting in a polygonal outline and irregular spaces between successive whorls. Stephenson (1941: 422) initially regarded the genus as having planispiral coils, but Haas (1943: 9) found that the Angolan species *A. angolatum* Haas was coiled helically. Most ribs in *Axonoceras* are bitubercu-

late, but non-tuberculate intermediaries do occur in the Texan species. In addition, Collignon (1971: 13) reported the occurrence of occasional stronger ribs in *A. multicostratum ellipticum* Collignon. Apart from the uncoiling and the recoiling of the inner whorls, the general shell shape of *Axonoceras* seems to be that of a low helix or loosely coiled spiral. Straight shafts and recurved hooks are unknown.

Scott & Cobban (1965) provided a reconstruction of the type species of *Exiteloceras*, *E. jennyi*. Gill & Cobban (1966: A32) and Scott & Cobban (1970: D73) defined the species as 'an aberrant ammonite that has juvenile whorls as straight limbs connected by semicircular bends, and later whorls loosely coiled in a plane without contact between adjacent whorls. Ornamentation consists of moderately coarse ribs, each of which terminates in a node at the margin of the venter'.

The irregularly coiled inner whorls of *Axonoceras* are compatible with the straight early limbs of *Exiteloceras*. Ornament and coiling in later whorls in both genera are similar, and it seems a reasonable procedure to regard *Axonoceras* as a junior synonym of *Exiteloceras*, as tentatively suggested by Wiedmann (1962: 198), and advocated by Matsumoto (1967: 340), Lewy (1969: 123), and Klinger (1976: 76).

Lewy (1969) described two new species of *Exiteloceras* from the Late Campanian of Israel, *E. unciforme* and *E. etegense*. The first shows scaphitoid coiling (uncoiling or recoiling) of the body chamber, and the latter irregular tuberculation on the venter, analogous to that found in *Neocrioceras* s.s. Spath, 1921. (Matsumoto & Morozumi (1980: 18), however, regard *E. etegense* and other species described by Lewy as possibly representing a new genus allied to *Neocrioceras* (*Schlueterella*) Wiedmann, 1962.) Wiedmann (1962: 206) also referred an uncoiled body chamber fragment from the Upper Campanian of Spain to *Exiteloceras*.

Thus interpreted, *Exiteloceras* cannot satisfactorily be separated from *Neancyloceras* as represented by the type species *Ancyloceras bipunctatum*. Furthermore the irregular crioceratid or aspinoceratid coiling in some *Ancyloceras bipunctatum* is similar to that found in *Exicrioceras* Anderson, 1958, type species *Exicrioceras ortigalitense* Anderson, 1958. The scaphitoid coiling of the body chamber of *Exiteloceras unciforme* Lewy easily connects the ancyloceratid coiling of some *Ancyloceras bipunctatum* with the closer, crioceratid coiling of typical *Exiteloceras*. The only real difference between *Neancyloceras* and *Exiteloceras* as interpreted above seems to be the differentiation of ribbing near or on the body chamber, but it is doubtful whether this merits separation, even at subgeneric level. If they were to be separated on this basis, *Axonoceras multicostratum ellipticum* Collignon with differentiated ribbing on the inner whorls would also have to be separated, thereby just increasing the list of heteromorph taxa based on insignificant differences.

Given that there appears to be no real difference between *Exiteloceras*, *Axonoceras*, *Exicrioceras*, and *Neancyloceras*, it is probably best to refer them all to the oldest available name, *Exiteloceras*.

Unfortunately detailed stratigraphic data are lacking, but it would be interesting to see the relationship between the ancyloceratid ('*Neancyloceras*' pars), ellipsoceratid ('*Excrioceras*'), scaphitoid (*Exiteloceras unciforme*) and closer-coiled crioceratid forms (e.g. *Exiteloceras jennyi*). Is there a trend towards recoiling, as observed in numerous heteromorph groups (see e.g. Wiedmann 1969) or is this merely part of intraspecific or generic variation or dimorphism?

ORIGIN AND PHYLOGENY

Matsumoto (1967: 339–40) considered it possible to derive *Exiteloceras* and *Axonoceras* from *Nostoceras* through widening of the apical angle of the helix. Indeed, forms such as '*Bostrychoceras polyplacum* Roemer ? var. *doneziana* Michailov' (Michailov 1951: 53, pl. 4 (figs 23–24)), which are coiled in a loose helix and with bituberculate ornament, are remarkably similar to the phragmone whorls of *Exiteloceras bipunctatum*. Similarly, the early straight whorls of forms such as *Didymoceras* cf. *D. nebrascense* (Lewy 1969: 116, pl. 1 (fig. 2)) are comparable to the early whorls of *Exiteloceras jennyi*.

As far as coiling and ornament are concerned, there are a number of features in common between *Exiteloceras*, *Neocrioceras*, and *Pseudoxybeloceras* that appear to be too related to be considered as merely homoeomorphic development (as tentatively suggested by Spath 1953: 17), and the author would rather derive these taxa from a common ancestor than from the contemporaneous nostoceratid forms as advocated by Matsumoto (1967).

Neocrioceras Spath, 1921, as interpreted by Wiedmann (1962: 205) comprises two subgenera, *Neocrioceras* s.s., type species *Crioceras spinigerum* Jimbo, 1894, with crioceratid coiling, simple ribbing and irregular tuberculation over the venter; and *N. (Schlueterella)*, type species *Ancyloceras pseudoarmatum* Schlüter, 1872. *N. (Schlueterella)* is a rather heterogenous group, but includes ancyloceratid to polyptychoceratid forms in which the tubercles are situated either on stronger or on looped ribs. Generally *Neocrioceras* s. l. can be separated from *Exiteloceras* by the presence of four rows of tubercles in the former but only two in the latter, but, as will be seen in *Pseudoxybeloceras*, the presence or absence of lateral tubercles may be of low systematic value. Points of similarity between *Exiteloceras* and *Neocrioceras* are: early helical coils occur in some *Exiteloceras* and in some *Neocrioceras*, e.g. *Neocrioceras* cf. *spinigerum* (Spath 1921: 52, pl. 7 (fig. 6)); ancyloceratid coiling occurs in some *Exiteloceras bipunctatum* as well as *N. (Schlueterella) pseudoarmatum* (Schlüter), although admittedly the latter already tends towards polyptychoceratid coiling; and irregular ornament occurs in both *Exiteloceras eteqense* Lewy and *N. (Neocrioceras) spinigerum* (Jimbo).

Closer resemblance is to be found in the genus *Pseudoxybeloceras* Wright & Matsumoto, 1954, as interpreted by Klinger (1976: 75), Matsumoto & Morozumi (1980), and (in essence) Ward & Mallory (1977), which includes

Christophoceras Collignon, 1969 (type species *Christophoceras ramboulai* Collignon, 1969) and *Parasolenoceras* Collignon, 1969 (type species *Parasolenoceras splendens* Collignon, 1969) as subgenera. The early whorls of *Pseudoxybeloceras* are unknown; thus far only J-shaped fragments have been found, but there is a distinct trend towards polyptychoceratid coiling in the later stages. *Pseudoxybeloceras* s.s. is quadrituberculate on every rib in the adult stage, but Matsumoto (1977: 346) has recently shown that the early stages of *Pseudoxybeloceras* (*P.*) *quadrinodosum* (Jimbo) lack the lateral tubercles, and that ornament in this respect is similar to that of *Exiteloceras*. *Pseudoxybeloceras* (*Parasolenoceras*) is apparently bituberculate throughout, like the juvenile stages of *Pseudoxybeloceras* (*Pseudoxybeloceras*) *quadrinodosum*, but already has distinct polyptychoceratid coiling in the early stages of growth. *Pseudoxybeloceras* (*Christophoceras*) has similar coiling and bituberculate ornament on the phragmocone, but develops major ribs on the body chamber and acquires lateral tubercles on these. The bituberculate ornament in *P.* (*Parasolenoceras*) and *P.* (*Christophoceras*) is analogous to that found in *Exiteloceras* in general, whereas differentiation of ornament on the body chamber of *P.* (*Christophoceras*) is similar to that of *Exiteloceras bipunctatum*.

The essential ingredients for the 'Bauplan' of these predominantly Santonian-Campanian genera *Exiteloceras*, *Neocrioceras*, and *Pseudoxybeloceras* were already present in the Turonian.

Parts of the early whorls of *Exiteloceras bipunctatum* are indistinguishable from the predominantly Turonian genus *Allocrioceras* Spath, 1926. Spath (1926: 81) had already noticed this, but regarded it as 'only superficial resemblance'. *Allocrioceras* consists mainly of helically coiled forms with undifferentiated, bituberculate ribbing. Differentiated ribbing does, however, occur in forms such as *Allocrioceras cuvieri* (Schlüter, 1872) and *A. turoniense* (Schlüter, 1872). *Ancyloceras paderbornense* Schlüter (1872: 97, pl. 30 (figs 1-2)) already has distinct *Neocrioceras* (*Schlueterella*) ornament. *Hamites multinodosus* Schlüter (1872: 106, pl. 32 (figs 1-2)) is part of a straight body chamber fragment, and shows ornament similar to that of *Christophoceras*.

Ward & Mallory (1977, test-fig. 2) show a lineage starting with *Neocrioceras* and *Pseudoxybeloceras* in the Turonian, trending towards more polyptychoceratid coiling through 'Cyphoceras' Ward & Mallory, 1977 (= *P.* (*Christophoceras*) and *P.* (*Parasolenoceras*)) to *Solenoceras* in the Maastrichtian. *Exiteloceras* first appears in the Upper Campanian, and it seems unlikely that its origins can be traced directly to *Neocrioceras* or *Pseudoxybeloceras* of the Turonian-Coniacian. Matsumoto (1959: 162) originally regarded *Exiteloceras* and *Pseudoxybeloceras* as having evolved in parallel or sister relationship from a 'plastic genus *Hyphantoceras*'.

Exiteloceras was probably derived from *Pseudoxybeloceras* s.s. in parallel with *P.* (*Christophoceras*) and *P.* (*Parasolenoceras*) in the Campanian (Fig. 10). In the latter two subgenera the trend is towards acquisition of polyptychoceratid coiling and reduction of the helical stage, whereas *Exiteloceras* retains the

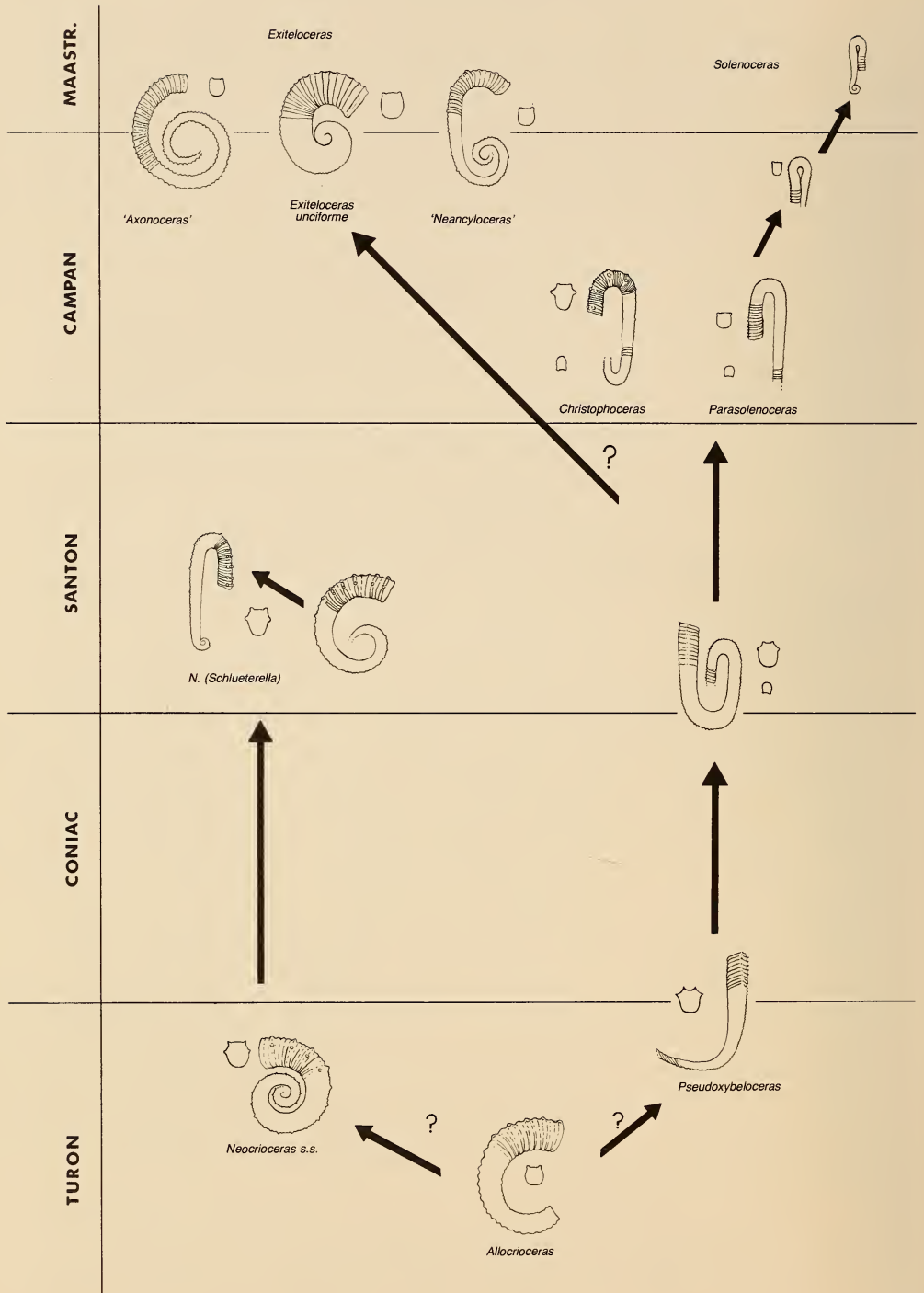


Fig. 10. Inferred phylogenetic relationship of *Exiteloceras*. Part of the diagram after Ward & Mallory (1977, text-fig. 2).

helical or crioceratitid stage to greater diameters and may possibly have solved hydrodynamic requirements by trending towards planispiral coiling.

LIMITS

Several species that have been referred to '*Neancyloceras*' probably do not belong there (see e.g. Naidin 1959; Wiedmann 1962; Blank *et al.* 1974), e.g. *Hamites wernickei* Wolleman, 1902, *Ancyloceras retrorsum* Schlüter, 1872, *Hamites interruptus* Schlüter, 1872, and *Hamites phaleratus* Griepenkerl, 1889.

Ancyloceras retrorsum lacks ventral tubercles throughout and is apparently a large glyptoxoceratid, as examination of Schlüter's types has shown, a view supported by Atabekian & Khakimov (1976: 61) and Blank *et al.* (1974: 168).

Hamites interruptus is thus far known only from small recurved fragments. The holotype (Fig. 8F–G) is still septate at the larger end, thus indicating that it is not a body chamber hook. The possibility cannot be excluded that this represents the early whorls of a form similar to *Exiteloceras jennyi*, but because of the polyptychoceratid coiling it is probably best placed in *Pseudoxybeloceras* (*Parasolenoceras*). Blank *et al.* (1974: 167) place it in *Solenoceras*.

Hamites wernickei is difficult to interpret. The small specimen with two shafts in contact, figured by Wolleman (1902, pl. 4 (fig. 5)) under that name, was previously regarded (Klinger 1976: 73) as better placed in *Solenoceras*. Should that specimen be conspecific with the larger hooks figured under that name by Wolleman (1902, pl. 4 (fig. 4), pl. 5 (figs 1–2)) or Pervinquièrè (1907: 86, pl. 3 (fig. 33)), the species may also be referred to *Pseudoxybeloceras* (*Parasolenoceras*).

Collignon (1971: 11, pl. 644 (fig. 2380)) described a small straight fragment from the Maastrichtian of Madagascar as *Neancyloceras ambindense*. In that specimen only every third rib is tuberculate. Collignon's generic allocation seems correct.

Blank *et al.* (1974: 169) refer *Hamites phaleratus* to *Neancyloceras*, but the figures of Griepenkerl (1889, pl. 11 (fig. 3), pl. 12 (figs 3–4)) suggest coiling to be polyptychoceratid, which would place it closer to *Pseudoxybeloceras* (*Parasolenoceras*) than to *Exiteloceras*.

Spath (1953: 49) mentions *Neancyloceras* from Angola, but this material has never been described, and the generic allocation cannot be verified.

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